ISOLATION AND SELECTION IN THE EVOLUTION OF SPECIES. THE NEED OF CLEAR DEFINITIONS

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THE discussion concerning the factors in organic evolution has been obscured by the diversity of meanings given to the same terms by different writers, and sometimes by the same writer. What do we mean by isolation, by selection, by environment, by evolution?

DIFFERENT MEANINGS GIVEN TO ISOLATION

I think that in Darwin's books isolation is always used to designate the prevention of free-crossing between different groups by means of factors lying outside of the groups, such as geographical barriers, but it has since been extended to mean the prevention of free-crossing by any means. Professor Kofoid, in his article in *Science* for March 29, 1907, gives the word this broader meaning in one place; but he must use it in a more limited way, when in the last sentence of his article, speaking of what DeVries finds in the elementary species "coincidently appearing" in the evening primrose, he says: "Isolation plays no part in their origin or continuance." I have not found any statement by DeVries maintaining that elementary species remain distinct forms from the original stock, when free-crossing with the original stock continues. In my volume on "Evolution, Racial and Habitudinal," pp. 5, 69–70, 155–156, I call attention to a mutation arising in certain species of snails, and probably producing complete isolation between the new form and the old, though both are occupying the same tree. The hermaphrodite snail is so constructed that it seems impossible for one of sinistral form to cross with one coiled in the opposite way; but in the Hawaiian Islands there are

a number of species presenting both forms. If direct crossing is impossible, it follows that the only chance for continued connection between the two forms is through the subsequent mutation of one or both of the forms; and we know that in some species this occurs in a small percentage of the offspring of each generation.

That isolation is not a necessary condition for the production of this mutation is shown by the fact that it rises suddenly in the midst of an intergenerating group; but the fact that it remains a distinct form, returning to the original form in only a small percentage of the offspring, seems to be due to the fact that by its structure it is prevented from crossing with the original stock. In other words, structural isolation, which is one form of autonomic isolation, produces racial demarcation and initial segregation, opening the way for intensive segregation, through the introduction of divergent forms of selection.

That natural selection is not the cause producing this mutation is shown by the fact that the old form and the new form are equally adapted to the same environment. I, however, maintain that the structural isolation produced by the mutation prepares the way for the introduction of permanently divergent forms of selection.

Different Forms of Selection

In the case of selection as in that of isolation, we find autonomic as well as heteronomic forms. Artificial selection as applied by man to the propagation of domestic plants and animals is a heteronomic factor; and in order to obtain permanently divergent races from the same stock, certain divergent variations or mutations are subjected to divergent forms of selection, while at the same time the different types are artificially isolated, unless there are autonomic factors holding the types apart. Such factors are preferential mating due to sexual and social instincts, or some degree of segregate fecundity; and in plants prepotence of pollen on the stigma of the same type, or flowering at different seasons. Natural selection is a form of heteronomic selection; for, as de-

scribed by Darwin, it is subject to change, only as the group is exposed to changed external conditions resulting in the survival and propagation of an average type differing more or less from the average birth type. Darwin also carefully described one form of autonomic selection, which he called sexual selection. In my volume on "Evolution, Racial and Habitudinal," I have called attention to social and filioparental selection, and several forms of impregnational selection, besides endonomic selection, in which the different methods of using the same environment, adopted by isolated branches of the same species, lead to the survival of different types of variation. These and other forms of autonomic selection must be considered in any complete analysis of the factors producing two or more divergent species from one original species.

VARIATION AND HEREDITY AND THEIR CONTROL

If my analysis of the factors producing divergence is correct, the active cause is found in the powers of variation and heredity possessed by the intergenerating group, while the conditions controlling, shaping and molding the variation and heredity are those that are designated by the terms isolation and selection. Isolation produces demarcational segregation; and divergent forms of selection in the isolated groups will produce intensive segregation, if isolation at the same time continues to hold the groups apart.

Romanes describes selection as a form of isolation, because its influence in controlling variation and heredity is due to its preventing those that survive from crossing with those that perish before propagating. That the influence of both isolation and selection is due to the prevention of free-crossing is certainly true, and, as I have further pointed out, both classes of factors cooperate in producing segregation. It think, however, that it is in better accord with the meaning that writers on natural history have usually given to the two terms to define isolation as the prevention of free-crossing between groups of

organisms *existing at the same time*. In certain cases the isolative process may be selective at the same time; and so demarcational and intensive segregation progress together; as is seen when the strong and courageous migrate together, leaving the weak and timid in the old habitat.

Diversity in the Use of a Complex Environment

An illustration of the wide divergence that may take place in a single family distributed over a small area is found in the Achatinellidæ, a family of snails found only on the Hawaiian Islands. Some genera of this family are found only on the ground, others chiefly on the trunks and branches of the trees, others on the leaves of the trees and shrubs. Ages of divergent evolution have made the individuals of each genus entirely incapable of crossing with those of other genera; but in the case of closely related varieties and species occupying different species of trees in the same valley the conditions are very different. These are cases in which the continued isolation can not be attributed either to external barriers or to physiological incompatibilities. The different methods of using the environment, whether due to habits or to inherited characters, is the real cause of the isolation. Again, of the ten genera of this family some are confined to one or two islands, though the vegetation and other conditions surrounding the family are much the same on the seven islands of the group. The condition explaining the small area occupied by any one of the five hundred species of this family is the limited power and opportunity for migration or transportation; and the great variety of types presented is undoubtedly due, first, to the power of variation possessed by isolated branches of the same species while using like environments in the same way; and second, to the variation in isolated groups introducing divergent methods of using the same complex environment and so subjecting themselves to divergent forms of selection, even when no external barriers hold them apart.

In *Science* for March 30, 1906, Dr. Ortmann refers to species of crawfish subjecting themselves to diverse con-

ditions, in isolated positions, by diversity in their "ecological habits." He describes them as "cases of ecological (or binomic) isolation, where no 'barriers' in the ordinary sense are present." In the relations of Hawaiian snails such cases are not infrequent. Even when the conditions in the environment with which the organism deals are extremely simple, the divergent groups of the original stock may adopt several different methods of dealing with these conditions, and with marked success in the use of each method. A fine illustration of this fact is found in the different species of Triposolenia, a genus of pelagic protozoa described by Professor C. A. Kofoid, in the University of California Publications, Zoology, Vol. 3, Nos. 6, 7 and 8, December 11, 1906. After considering the nature of the several different types found coexisting in the same region, "in the surface waters of the sea," he concludes that, "The utility of each of the complexes of characters is sufficient for their preservation without the necessity of calling in *natural selection* to account for their differentiation and continuance." (See pp. 121, 123.)

CAUSES OF THE EARLIER FORMS OF DIVERGENCE

In the discussion that has appeared in *Science* during the past two years, the chief interest has centered around the question of the causes of the earliest forms of divergence. One method of inquiry has been to observe whether in a given family of organisms the most nearly allied species and races are found in the same or in separate districts. If with great uniformity the nearest allies are found in separate districts, there is good reason to believe that initial demarcation has been due to geographical barriers, or at least to local isolation. If the analysis already given is correct, the first step in divergence must be sought either in some process of migration, or transportation producing local isolation; or in some variation in form, or habits of feeding, or instincts for mating, or time of flowering, or in prepotence of pollen, or in some other quality producing incompatibilities, and so producing

autonomic isolation. In such creatures as snails, it would seem that the different forms of impregnational isolation do not often arise before a considerable degree of divergence has been reached; for usually the most nearly related races, or varieties of Achatinella are found on separate groves of the same species of trees, in different parts of the same valley; while the most closely related groups of varieties, that are classed as separate species, are usually found in separate valleys; though sometimes in the same valley, but living on different species of trees.

In the case of plants, I have seen closely related species growing beside each other, and in some such cases they are found to flower at different months of the year, and in other cases it would probably be found that they are held apart by the prepotence of pollen of a given species on stigmas of the same species. In some of these cases where the present form of isolation is undoubtedly autonomic, it may be impossible to say whether the new type was not first developed in a few individuals, that for a generation or two were partially isolated geographically or locally in some sheltered nook.

Do New Types Continue in Spite of Free-Crossing?

As we have already shown in certain species of Hawaiian snails, a sudden mutation may arise, which by its very constitution is prevented from crossing with the parent stock; and in such cases it is evident that a permanent type may begin with the mutation. But is there any proof that a mutation that freely crosses with the original stock will remain unchanged, each type thriving and remaining unblended with the other? If the mutation is the dominant form, it may be granted that it will in time overwhelm the original form; but can two closely related races or species freely cross with each other, for many generations, without either type being affected by the process? For an answer to this question I would refer the reader to an article by Robert Greenleaf Leavitt in The American Naturalist for April, 1907. On pp. 214–217 he gives quotations from Professors Davenport,

Castle and Forbes, showing that "Everywhere unit characters are changed by hybridizing." This testimony is chiefly from those who have experimented with the crossing of animal forms, but even in the case of plants, there is reason to believe that when free-crossing continues divergence is checked. There is reason to believe that even with plants the controlling factor in each case of continuously divergent evolution is either some form of heteronomic isolation or some form of variation introducing autonomic isolation.

MORITZ WAGNER'S THEORY AND MY THEORY WERE ISOLATED AND DIVERGENT FROM THE BEGINNING

Moritz Wagner, in his "Law of the Migration of Organisms," was the first to insist on the importance of geographical isolation as a factor in evolution, but when he asserted that without geographical isolation natural selection could have no effect in producing new species he went beyond what could be sustained by facts. My own theory, though it did not take form till four years later, was reached without any knowledge of his, and therefore in complete isolation from his; and when they came together for comparison they were found to be quite divergent.

In March, 1868, Moritz Wagner read a paper before the Royal Academy of Sciences at Munich on "The Law of the Migration of Organisms," and in 1873 an English translation of a fuller paper by him entitled "The Darwinian Theory and the Law of the Migration of Organisms" was published by Edward Stanford, of London. It was through this pamphlet that I became acquainted with his theory concerning the impossibility of the production of new species except when and where migration establishes a colony geographically isolated from the original stock. In this paper we read: "The constant tendency of individuals to wander from the station of their species is absolutely necessary for the formation of races and species" (p. 4). "Where there is no migration, that is, where no isolated colony is founded, natural

selection can not take place'' (p. 59). These and many other passages of similar import indicate how fully he recognized the importance of isolation, and how at the same time his theory was a denial of some of the facts in the origin of species. The following are some of the facts with which his general theory as well as his special statements were in conflict:

1. That, through change of climate and of other conditions due to geological changes, the whole fauna and flora of an island like Iceland might be subjected to new forms of selection producing a complete change of many species into new species, without any chance for migration. After the publication of my article in *Nature,* July 18, 1872, in which I emphasized the importance of isolation, I met Darwin at his home, and he called my attention to Wagner's theory, and suggested that it did not correspond with the facts of nature, especially on this point.

2. That the influence of geographical isolation in producing divergence, and in opening the way for selection to cooperate in producing divergence, is wholly due to its prevention of free-crossing, and that the same result may, in various ways, be brought about by divergent habits or instincts, or other incompatibilities, while the isolated groups remain in the original habitat of the species.

3. That divergence does not necessarily require the influence of different forms of selection.

4. And that different forms of selection do not necessarily depend on exposure to unlike environments; for diversity in the forms of selection may be due to diversity in the methods of using the same environment adopted by isolated branches of the same species.

In August, 1872, I read before the British Association for the Advancement of Science a paper on ''Diversity of Evolution under One Set of External Conditions,''[1] in which the conditions just mentioned were briefly stated. In two subsequent papers entitled ''Divergent Evolution through Cumulative Segregation,'' and ''Intensive Seg-

[1] This paper was soon after published in the Linnean Society's *Journal,* Zoology, vol. XI, pp. 496–505.

regation,'' read before the Linnean Society in 1887 and 1889, and published in their *Journal,* the subject was more fully discussed, and since then in my volume on ''Evolution, Racial and Habitudinal,'' published by the Carnegie Institution, my view of the factors of organic evolution has been presented, with special relation to their interaction on each other, and the close correlation between the evolution of habits and the evolution of racial characters. It is to this last-mentioned phase of the subject that I have hoped that I might call special attention. I regard this influence of acquired habits in the control of the forms of selection as of great importance, especially in the evolution of the higher classes of animals, and in the races of mankind.

MEANING OF THE TERM ENVIRONMENT

In all my discussions, I have been careful to give a uniform meaning to the term environment. When treating the evolution of species, or of smaller groups of intergenerating organisms, the environment is, in my language, always the set of influences lying outside of the group under discussion, and is never used to designate the influence of one part of the group upon another part, as, for example, the influence of parents upon offspring, of males upon females, of the strong upon the weak. In the generalizations made by some writers, it is impossible to decide whether the environments referred to are intended to include these reflexive influences or not. But even with the broadest interpretation of the term environment, I can not accept the statement often made that there is no divergence in branches of the same species unless they are exposed to different environments.

Such a conclusion seems to be based on the assumption that all transformation in organisms is due to adaptations giving more or less advantage to the forms that survive, and ignores the fact that in many species there are countless variations of a non-utilitarian character. It also fails to recognize the fact that isolated groups of individuals of the same variety, exposed to the same external

environment, and also to the same internal influences producing selection, may still, before many generations have passed, adopt different methods of dealing with the external environment, or introduce divergent forms of sexual or social selection, or of some other form of reflexive selection. The divergence, in such cases, is explained by the power of the species to vary, and by the probability that the variation will introduce new methods of meeting surrounding conditions. F. W. Headley, in his volume on "Problems of Evolution" (on pp. 146–149), gives illustrations of how branches of the same species may adopt "*alternative methods of adjustment to the same environment,*" and yet in the same book (on p. 103) we read: "If the environment remains unchanged, evolution ceases," and on p. 153—"Nothing but change of environment can lead to further evolution." His mind seems to cling to the old statements of general laws, though he has come to recognize a class of facts that are quite at variance with these old statements.

It therefore appears that we need not only a clear and consistent use of terms, but a clear and consistent statement of the facts of the organic world, in their bearing upon the changes that take place in organisms. I have carefully studied O. F. Cook's article in *Science* of March 30, 1906, and his previous papers to which he refers in that article. The chief difference in our estimates of the factors of evolution seems to me to result from a difference in the meanings that we give to the word evolution. In my use of the word all changes and divergences in the inherited and acquired characters of organisms are included. The chief factors I find to be variation and heredity in an intergenerating group moulded and controlled by isolation and selection. Fuller statements will be found in my book on "Evolution, Racial and Habitudinal," pp. 60, 79–80, and 138. Of these factors Dr. Cook says that variation and intergeneration relate to evolution, but isolation and selection, though "factors of species-formation, are not at all factors of evolution." It is evident that this difference in our enumeration of the factors of evolution is due to the different meanings that we give to the term evolution.